

# COMPETITION FOR LIGHT AND A DYNAMIC BOUNDARY BETWEEN CHAPARRAL AND COASTAL SAGE SCRUB

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## ABSTRACT

A sharp boundary between mature stands of *Ceanothus* chaparral and coastal sage scrub was found in the Santa Monica Mountains in coastal southern California. The presence of numerous dead coastal sage scrub species in the understory of the chaparral suggests that the chaparral has been progressively invading the coastal sage scrub during the last several fire cycles.

McPherson and Muller (1967) demonstrated that light competition occurred between the chaparral shrub, *Ceanothus cuneatus*, and the drought-deciduous shrub, *Salvia leucophylla*, at an inland site in southern California. Seedlings of both species apparently established together following a fire; however, after 26 years, the evergreen shrubs had overtopped and suppressed the drought-deciduous shrubs. Using both field and lab experiments, McPherson and Muller (1967) eliminated the role of phytotoxins, soil moisture, and soil nutrients in creating the observed pattern. They showed that the taller *Ceanothus* shrubs interfered sufficiently with light reaching shorter *Salvia* shrubs to eliminate them after 26 years.

In this paper, I report a similar case of apparent light competition between the chaparral shrub, *Ceanothus megacarpus*, and several drought-deciduous shrub species at a coastal site in southern California. I also hypothesize about the long-term dynamics of the chaparral/coastal sage scrub ecotone at this site.

At mid-elevations (100–300 m) along the immediate coast of the Santa Monica Mountains 50 km northwest of Los Angeles, mature stands of chaparral and coastal sage scrub occur together and often form a mosaic across the landscape. The chaparral is dominated by *Adenostoma fasciculatum* or *Ceanothus megacarpus* (Bauer 1936), whereas the coastal sage scrub is comprised of the common drought-deciduous shrubs *Artemisia californica*, *Salvia leucophylla*, and *S. mellifera* (Kirkpatrick and Hutchinson 1977, Gray and Schlesinger 1981, Westman 1981). Where the two vegetation types meet, there often is a sharp boundary between them, even in the absence of obvious edaphic or geologic discontinuities. This pattern suggests that biotic interactions, historic factors (fire, grazing, human activity), or both, may be important.



FIG. 1. Adjacent, even-aged stands of *Ceanothus* chaparral (dark region, left foreground) and coastal sage scrub (light regions) in the Santa Monica Mountains of southern California. Mixed *Adenostoma* chaparral is in the upper left. There is a road cut in the foreground.

## METHODS

Adjacent, mature stands of chaparral and coastal sage scrub, located in the Santa Monica Mountains (150 m elevation and 3 km from the ocean), were the site of a three-year comparative study of productivity and nutrient cycling (Gray 1982, 1983) and are shown in Fig. 1. Wildfire burned through the canyon and study site in 1956 according to local residents and California Department of Park and Recreation officials.

To determine canopy cover and density of individual species in the chaparral and coastal sage scrub, 50-m sample transects were conducted through the center of each community. One-hundred paired,  $1 \times 1$ -m quadrats were sampled along each transect line. The presence of all live and dead individuals of all shrub species in each quadrat was recorded. Canopy cover was estimated by measuring the canopy projection of each species along a 50-m tape (line intercept method). Relative cover was calculated for each species as the total distance covered by the canopy of a species divided by the total distance covered by the canopies of all species.

Dead shrubs of all species were remarkably intact, particularly in the chaparral: all were rooted, relatively unweathered, and undisturbed by animal activity. Each dead shrub was identified to species

by using species characteristics of branching geometry (*Salvia leucophylla*, *Eriogonum parvifolium*), stem morphology (*Ceanothus megacarpus*), and bark texture (*Artemisia californica*, *Adenostoma fasciculatum*, *Eriophyllum confertiflorum*).

Eighteen whole shrubs of *Ceanothus megacarpus* were harvested in June 1979 using a stratified-random selection (Gray 1982). The age of each shrub was determined by ring counts at the base of the stems.

## RESULTS AND DISCUSSION

The chaparral stand was completely dominated by *Ceanothus megacarpus* in terms of cover and density (Table 1). Living *Ceanothus megacarpus* shrubs were 4–6 m in height and the foliage was concentrated in the upper 75 cm. The canopy was completely closed. Numerous, attached dead branches were present in the lower portions of the shrubs, a characteristic of other *Ceanothus* species in the chaparral (Keeley 1975).

The age of the living *Ceanothus* shrubs ranged from 20–22 years in the sample shrubs. *Ceanothus megacarpus* does not crown sprout and reproduces only by seed after a fire. It typically forms rapidly growing stands of even-aged individuals (Schlesinger and Gill 1980).

Several other species were present in the chaparral, but were few in number (Table 1) and 1–1.5 m shorter than *Ceanothus megacarpus*. Several of these species, including *Eriogonum*, *Cercocarpus*, and *Adenostoma* exhibited broad, etiolated leaves typical of shade plants (Boardman 1977), appeared to be growing slowly, and did not flower during the three years of the study.

Numerous standing dead individuals of both evergreen and drought-deciduous species were also in the understory of the chaparral (Table 1). The dead *Ceanothus megacarpus* shrubs were 10–12 years old and small in stature. These plants appeared to be aggregated, as suggested by the high standard deviation associated with their density values (Table 1). These dead individuals of *Ceanothus* were apparently eliminated by intra-specific competition for water during early stand development as shown by Schlesinger and Gill (1980).

The drought-deciduous species in the understory of the chaparral were the same species that comprised the adjacent coastal sage scrub (Tables 1, 2). All individuals of coastal sage scrub species in the chaparral were dead with the exception of *Eriogonum* and *Yucca*. In contrast, mortality in the coastal sage scrub community was only a small percentage of the total number of shrubs and was restricted to *Artemisia* and *Salvia* (Table 2). The density of dead *Artemisia* and *Salvia* shrubs in the chaparral was significantly less than for live shrubs in the coastal sage scrub. Only 10% of the dead *Artemisia* and *Salvia* shrubs in the chaparral appeared to have arisen from crown sprouts, compared to 33% of the live shrubs in the coastal sage scrub.

TABLE 1. PERCENT RELATIVE COVER AND ABSOLUTE DENSITY OF INDIVIDUALS IN THE *Ceanothus* CHAPARRAL. Standard deviations (S.D.) are given for the density values, n = 100.

Species	Evergreen (E) or drought-deciduous (DD) leaves	Relative cover (%)	Density (individuals per square meter)	S.D.
Live plants				
<i>Ceanothus megacarpus</i>	E	99	2.67	2.68
<i>Adenostoma fasciculatum</i>	E	1	0.13	0.43
<i>Eriogonum parvifolium</i>	DD	1	0.09	0.24
<i>Yucca whipplei</i>	E	1	0.07	0.24
<i>Ceanothus spinosus</i>	E	1	0.03	0.23
<i>Cercocarpus betuloides</i>	E	1	0.02	0.08
<i>Rhus laurina</i>	E	1	0.01	0.07
Dead plants				
<i>Ceanothus megacarpus</i>	E	—	1.73	3.27
<i>Adenostoma fasciculatum</i>	E	—	0.30	0.38
<i>Eriophyllum confertiflorum</i>	DD	—	0.30	0.47
<i>Eriogonum parvifolium</i>	DD	—	0.25	0.43
<i>Artemisia californica</i>	DD	—	0.18	0.42
<i>Salvia leucophylla</i>	DD	—	0.10	0.20
<i>Yucca whipplei</i>	E	—	0.01	0.07
<i>Ceanothus spinosus</i>	E	—	0.01	0.07

The presence of dead coastal sage scrub species in the understory of the chaparral suggests a case of light competition similar to that described by McPherson and Muller (1967). After a previous fire, both evergreen and drought-deciduous species established side by side as seedlings, or in the case of *Artemisia* and *Salvia*, as both seedlings and crown sprouts (Westman et al. 1981). By 7 to 10 years, *Ceanothus* shrubs were tall enough to overtop the coastal sage scrub species. Eventually, the greater biomass and height of the *Ceanothus* shrubs interfered sufficiently with light reaching the smaller drought-deciduous shrubs to suppress and eliminate them. The great attenuation of light by the canopy in mature stands of *Ceanothus megacarpus* has been documented by Schlesinger and Gill (1980), who found light levels well below that needed for net photosynthesis by the related chaparral shrub, *C. greggii*. Indeed, the decrease of available light beneath the canopy during stand development in *Ceanothus megacarpus* is manifest in the death of lower branches (Gray 1982).

Several results of McPherson and Muller (1967) are different from the situation described here. They reported that two cohorts of *Ceanothus cuneatus*, aged 16 and 26 years, were present in their chaparral stand. *Ceanothus* shrubs in this study were even-aged. *Ceanothus megacarpus* seeds require heat alteration for germination (Hadley 1961),

TABLE 2. PERCENT RELATIVE COVER AND ABSOLUTE DENSITY OF INDIVIDUAL SHRUBS IN THE COASTAL SAGE SCRUB. Standard deviations (S.D.) are provided for density values,  $n = 100$ . <sup>1</sup> Grasses: *Stipa lepida*, *Elymus condensatus*, *Bromus* sp.; herbs: *Castilleja affinis*, *Eriophyllum confertiflorum* seedlings, *Galium* sp., *Haplopappus squarrosus*, *Paeonia californica*, *Pityrogramma triangularis*.

Species	Evergreen (E) or drought- deciduous (DD) leaves	Relative cover (%)	Density (individuals per square meter)	S.D.
Live plants				
<i>Salvia leucophylla</i>	DD	49	0.98	1.24
<i>Artemisia californica</i>	DD	29	0.81	1.64
<i>Yucca whipplei</i>	E	7	0.07	0.32
<i>Eriogonum parvifolium</i>	DD	4	0.20	0.40
<i>Eriophyllum confertiflorum</i>	DD	2	0.55	0.32
Herbs and grasses <sup>1</sup>	—	9	—	—
Dead plants				
<i>Artemisia californica</i>	DD	—	0.13	0.43
<i>Salvia leucophylla</i>	DD	—	0.01	0.07

and successful germination is unlikely to occur between fires; hence, only a single cohort of *C. megacarpus* establishes after a fire. McPherson and Muller (1967) also found that most, if not all, of the *Salvia* shrubs in the chaparral understory were still alive and flowering after 26 years. The absence of any living *Salvia* shrubs in the *C. megacarpus* stand suggests that suppression at this site was more rapid. Annual production in *C. megacarpus* chaparral exceeds all reported values for California chaparral and other mediterranean-type ecosystems of the world (Gray 1982) and may facilitate a rapid overtopping of drought-deciduous shrubs.

#### HYPOTHESIS OF STAND DYNAMICS

Two mutually exclusive hypotheses can be proposed to explain the observed pattern in the chaparral: (1) The present stand of *Ceanothus* has persisted through many fires with a similar structure and biomass, and the dead, drought-deciduous species in the understory are only the remnants of early successional species that temporarily occupied the site. This successional relationship between coastal sage scrub and chaparral has been described in other chaparral communities (Cooper 1922, Wells 1962, Hanes 1971, 1977). (2) The present chaparral stand was occupied by a mature coastal sage scrub community immediately prior to the last fire. The latter community was completely eliminated by a single invasion of *Ceanothus* as a result of a large influx of seed before or immediately after the fire.

The data and field observations are not consistent with either hypothesis. The existence of *Artemisia* and *Salvia* shrubs that arose from crown sprouts in the chaparral understory indicates that these individuals had been present for at least two fire cycles. Hence, these species do not appear to be temporary, early successional occupants of the chaparral stand. It is also unlikely that the present chaparral stand developed en masse after the last fire, because there is no adjacent, upslope chaparral stand of *Ceanothus* to provide a large seed source (Fig. 1). Indeed, the only upslope chaparral stand is dominated by *Adenostoma* and it is separated from the *Ceanothus* stand by an 80-m strip of coastal sage scrub (Fig. 1).

A third hypothesis to explain the sharp boundary and dead coastal sage scrub species in the chaparral is the slow, progressive, invasion of the coastal sage scrub stand by *Ceanothus* after several fire cycles. In this scenario, a few isolated *Ceanothus* initially became established in the coastal sage scrub stand after a previous fire. These shrubs probably arose from seed that was dispersed by downslope movement or animal activity. Such isolated *Ceanothus* shrubs are now present around the edges of the coastal sage scrub stand (Fig. 1). These scattered shrubs then produced a large seed crop, which in turn gave rise to many more shrubs after the next fire. *Ceanothus* species in the chaparral have been observed to produce up to 835 seeds/m<sup>2</sup> in a single year (Keeley 1977). Given this potential for high seed production, only a few fire cycles may be necessary to permit the development of a relatively pure stand, which in turn would suppress and eliminate drought-deciduous shrubs.

The speed and extent of an invasion by *Ceanothus* would be affected by a variety of factors including variation in seed production, viability of stored seed in the soil, and the degree of seed predation. *Ceanothus* species in the chaparral vary greatly in annual seed output and appear to have very little seed storage potential in the soil (Keeley 1977). Hence, a fortuitous combination of an abundant seed crop followed by a fire and low seedling mortality would be necessary for this encroachment by *Ceanothus* to occur.

The data suggest that *Ceanothus* shrubs are capable of invading coastal sage sites in the Santa Monica Mountains of southern California, resulting in the extension of *Ceanothus* chaparral into lower elevations more typical of coastal sage scrub (Harrison et al. 1971). Thus, in contrast to a recent documentation of a coastal sage scrub/chamise chaparral boundary in interior San Diego County that has been stable for more than 60 years (Bradbury 1978), I suggest that the boundary between *Ceanothus* chaparral and coastal sage scrub is a dynamic one, arising from competitive interactions after fires.

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